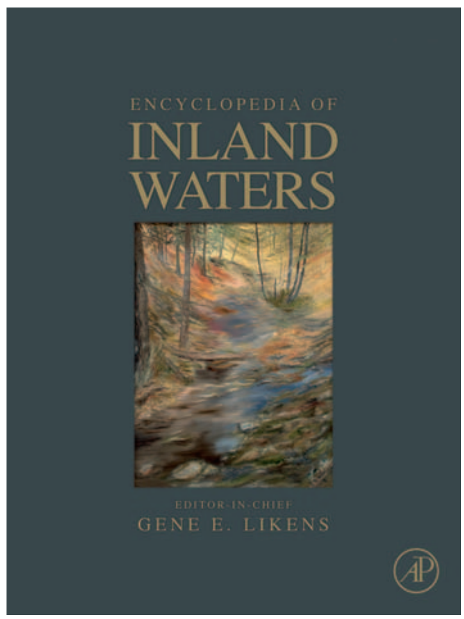

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Lakes of Antarctica

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Introduction

The evolutionary history of Antarctic lakes reflects the history of the continent itself. More than 170 Mya, Antarctica was part of the supercontinent Gondwana. Over time Gondwana broke apart and Antarctica, as we know it today, was formed around 25 Mya. During its evolution, the continent underwent numerous climate shifts. Around 65 Mya, Antarctica still had a tropical to subtropical climate, complete with an Australasian flora and fauna. Ice first began to appear around 40 Mya. The opening of the Drake Passage between Antarctica and South America around 23 Mya resulted in the Antarctic Circumpolar Current, which effectively isolated the advection of lower latitude warm water to the region, leading to continent-scale glaciations that now typify Antarctica. The period between 14.8 and 13.6 Mya (mid Miocene) saw an important change in the landscape evolution. During this time, the linked climate-and-glacial system changed from one dominated by intermittent fluvial erosion and wet-based glaciation, to one featuring a largely cold-based ice sheet, with cold-based alpine glaciers in the hyperarid, cold-desert conditions of the Transantarctic Mountains. The last Antarctic glaciation reached a maximum around 18 000 years ago, a period when the present ice sheet was much thicker and extended out to the edge of the continental shelf. The icecaps of offshore islands were similarly more extensive. These extensive ice sheets retreated during the late Pleistocene and have remained relatively stable during the current Holocene epoch. As a result of this temporal evolution, we now see lakes distributed on maritime islands, along the margins of the continent in ablation regions, and subglacially, beneath the thick ice sheet. All these lakes reflect, to varying degrees, the legacy left by past geological and climatological conditions.

This article describes the formation, distribution, and diversity of lakes in selected regions in Antarctica where focused research efforts have occurred. Although no subglacial lakes have been sampled directly, we present an overview of what is known about them, with a focus on Lake Vostok, the largest of these lakes.

The Antarctic Continent: An Overview of Lake Regions

Antarctica comprises more than 14×10^6 km^2, making it the fifth largest continent. Physically, it is divided into West Antarctica and East Antarctica by the Transantarctic Mountains. Antarctica is the coldest place on Earth with about 98% of the continent covered by permanent ice, which averages 2.5 km in thickness. The continent holds 70% of all the fresh water on Earth, in the form of ice. Average winter temperatures approach −75°C in the continental interior and −25 °C along the margins. The average temperatures during summer are considerably warmer, reaching −35 and −10 °C for the same regions. Despite the subzero temperatures and thick ice sheets, numerous lakes exist on the Antarctic continent (Figure 1). Except for the subglacial lakes, Antarctic lakes are confined to the ice free coastal regions. The surface lakes range in latitude from 60°43′ S (Signy Island) to 77°30′ S (McMurdo Dry Valleys) (Table 1). The air temperatures and ice cover characteristics of the lakes reflect this latitudinal location with lakes at lower latitudes having thinner and shorter seasonal ice covers and higher productivity.

Subglacial Lakes

Location The earliest evidence of subglacial lakes was from Russian aircraft pilots flying missions over the Antarctic continent, claims subsequently verified by airborne radio–echo sounding during the 1960s and 1970s. We now know that more than 150 lakes exist beneath the Antarctic ice sheet (Figure 1), many of which may be connected by large subglacial rivers. Approximately 81% of the detected lakes lie at elevations less than ~200 m above mean sea level, while the majority of the remaining lakes are 'perched' at higher elevations. Sixty-six percent of the lakes lie within 50 km of a local ice divide and 88% lie within 100 km of a local divide. The high density of lakes in the Dome-C region implies that they may be hydrologically connected within the same watershed and would be an important system to study from the standpoint of subglacial hydrology and biological and geochemical diversity.

Formation and diversity The association of subglacial lakes with local ice divides leads to a fundamental question concerning the evolution of subglacial lake environments:

Does the evolving ice sheet control the location of subglacial lakes or does the fixed lithospheric character necessary for lake formation (e.g., basal morphology,

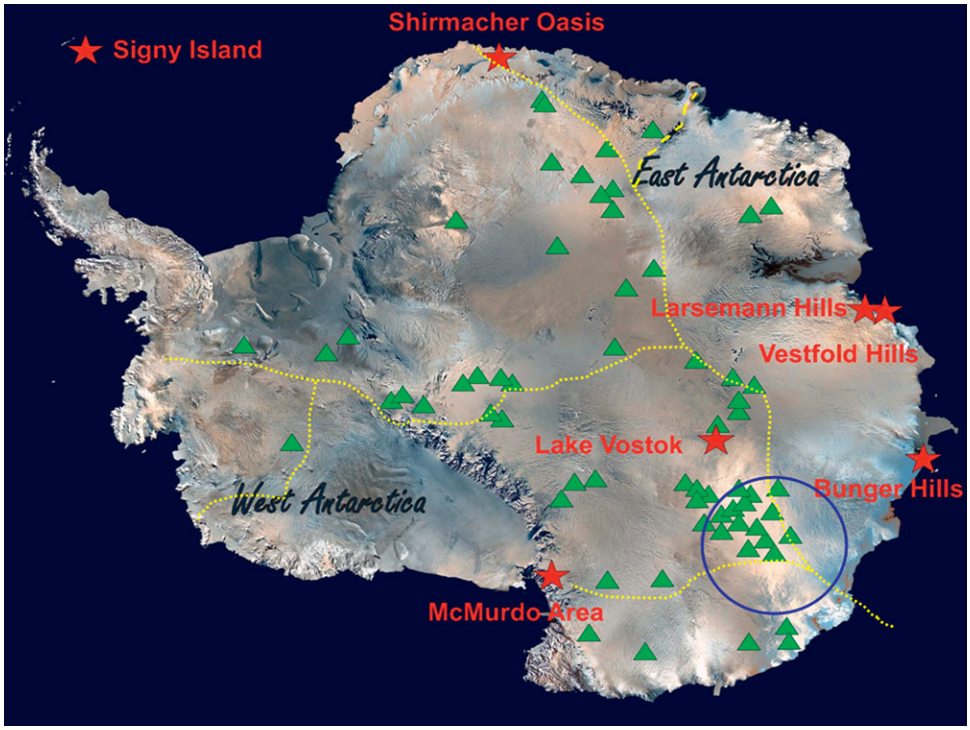

Figure 1 Locations of the lakes discussed in the text. Red stars show the locations of specific lakes or regions; triangles denote the location of known subglacial lakes; yellow dashed lines represent the approximate location of several of the major ice divides on the continent; blue circle denotes the Dome-C subglacial lake cluster.

Table 1 Location, air temperature, and ice cover characteristics of selected lake regions discussed in this article

District	*Latitude*	*Mean temperature*			*Ice cover*	*Notes*
		Annual	*Summer*	*Winter*		
Subantarctic Islands						
Signy Island	60°43′ S	−4.2	1.4	−9.6	Variable (8–12 mo, 1–2 m)	Maritime climate zone
Continental ice-free zones						
Shirmacher Hills	70°45′ S	−10.8	−2.0	−16.1	Permanent (∼3 m)	Freshwater and epishelf lakes
Larsemann Hills	69°03′ S	−10.5	4.0	−15.0	Variable (8–10 mo), ∼2 m	Freshwater lakes
Vestfold Hills	68°33′ S	−10.0	−0.9	−16.9	Variable (8–10 mo), 0.5–2 m	Saline lakes formed by isostatic rebound
Bunger Hills	66°17′ S	−9.0	0.4	−16.3	Variable (8–12 mo, 2–4 m)	Many tidally influenced epishelf lakes
McMurdo Dry Valleys	77°30′ S	−17.7	−3.1	−25	Permanent (4–19 m)	Many chemically stratified with ancient bottom water brines

Sources
Jacka TH, Budd WF, and Holder A (2004) A further assessment of surface temperature changes at stations in the Antarctic and Southern Ocean, 1949–2002. *Annals of Glaciology* 39: 331–338.
Simmons GM, Vestal JR, and Wharton RA (1993) Environmental regulators of microbial activity in continental Antarctic lakes. In: Friedmann I (ed.) *Antarctic Microbiology*, pp. 491–451. New York: Wiley-Liss.
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Gibson JAE and Anderson DT (2002) Physical structure of epishelf lakes of the southern Bunger Hills, East Antarctica. *Antarctic Science* 14(3): 253–261.

geothermal flux or the nature of sub-ice aquifers) constrain the evolution of ice sheet catchments? With the exception of central West Antarctica (where lakes are few), we know little about either the lithospheric character along these catchment boundaries or the history of their migration, given by layering within the ice sheet. Subglacial lake environments rest at the intersection of continental ice sheets and the underlying lithosphere. This unique location sets the stage for generating a spectrum of subglacial environments reflective of the complex interplay of ice sheets and the lithosphere.

Antarctic subglacial lakes have been categorized into three main types: (1) lakes in subglacial basins in the ice-sheet interior; (2) lakes perched on the flanks of subglacial mountains; and (3) lakes close to the onset of enhanced ice flow. The bedrock topography of the ice-sheet interior involves large subglacial basins separated by mountain ranges. The lakes in the first category are found mostly in and on the margins of subglacial basins. These lakes can be divided into two subgroups. The first subgroup is located where subglacial topography is relatively subdued, often toward the center of subglacial basins; the second subgroup of lakes occurs in significant topographic depressions, often closer to subglacial basin margins, but still near the slow-flowing center of the Antarctic Ice Sheet. Where bed topography is very subdued, deep subglacial lakes are unlikely to develop. Lake Vostok (surface area of ~14 000 km^2, maximum depth ~800 m; volume ~5400 km^3) is the largest known subglacial lake and the only one that occupies an entire section of a large subglacial trough. Theoretical models reveal that the subglacial environment may hold ~10% of all surface lake water on Earth, enough to cover the whole continent with a uniform water layer with a thickness of ~1 m. These models further reveal that the average water residence time in the subglacial zone is ~1000 years.

Much attention is currently focused on the exciting possibility that the subglacial environments of Antarctica may harbor microbial ecosystems isolated from the atmosphere for as long as the continent has been glaciated (20–25 My). The recent study of ice cores comprised of water from Lake Vostok frozen to the overlying ice sheet has shown the presence, diversity, and metabolic potential of bacteria within the accreted ice overlying the lake water. Estimates of bacterial abundance in the surface waters range from 150 to 460 cells ml^{-1} and small subunit rDNA gene sequences show low diversity. The sequence data indicate that bacteria in the surface waters of Lake Vostok are similar to present day organisms. This similarity implies that the seed populations for the lake were incorporated into the glacial ice from the atmosphere and were released into the lake water following the downward transport and subsequent melting from the bottom of the ice sheet. Subglacial lakes present a new paradigm for limnology, and once sampled, will produce exciting information on lakes that have been isolated from the atmosphere for more than 10 My.

Signy Island, South Orkney Islands

Location Signy Island (60°43′ S, 45°36′ W) is a 20 km^2 island in the South Orkney archipelago. It lies at the confluence of the ice-bound Weddell Sea and the warmer Scotia Sea, and its climate is influenced by the cold and warm air masses from these two areas. The lakes on Signy Island share characteristics of Antarctic and subAntarctic environments, a fact reflected in the diverse flora and fauna. This region of the continent has been ice free for the past 6000 years and is referred to as the maritime Antarctic zone, with an annual mean air temperature near −4 °C. The island is small (7×5 km^2; surface area 19.9 km^2) and has relatively little relief (maximum elevation 279 m). Most of the 17 lakes on Signy Island lie in the valleys and plains of the narrow, coastal lowland, which is usually snow free during the summer. The lakes on Signy Island that have received extensive study include Heywood, Sombre, Amos, and Moss. Radiocarbon dates on basal sediment from the lakes on Signy Island show that these lakes did not exist more than ~12 000 years ago, making them similar in age to many of the continental lakes.

Formation and diversity These lakes share a common geology but cover a wide range of physical, chemical, and biological properties. Sombre lake is an ultraoligotrophic system receiving no significant nutrient input. The inflows consist primarily of snow melt streams which are frozen for 8–9 months in a year. As a result, the water column is relatively clear and most of the primary production comes from benthic cyanobacterial mats. Many of the lakes are suffering animal-induced (fur seal) eutrophication with Amos and Heywood lakes being the most severely affected. Unlike Sombre lake, the water column of Amos lake develops a dense phytoplankton bloom during spring and summer in response to elevated nutrient enrichment.

A summary of data averaged over a 6-year period (Table 2) reveals that the pH in these lakes is circumneutral, whereas the conductivity varies from 40 to 233 μS cm^{-1}, reflecting waters of extremely low to moderate ionic strength. The chlorophyll *a* levels generally increase with conductivity and represent waters ranging from mesooligotrophic to mesoeutrophic. Levels exceeding 10 μg l^{-1} chlorophyll *a* in Heywood lake result from wildlife-induced nutrient loading. Dissolved inorganic nitrogen (DIN; $NO_3^- + NH_4^+$) and soluble reactive phosphorus (SRP) concentrations also vary considerably across the lakes on Signy Island, reflecting various degrees of nutrient loading and biological consumption. The ratio of DIN:SRP ranges from 3.6 to 445.3 revealing a wide range of potential

Table 2 Selected chemical and biological properties from 14 lakes on Signy Island

Lake	*Depth (m)*	*pH*	*Conductivity (μS cm⁻¹)*	*Chl a (μg l⁻¹)*	*Cl⁻ (mg l⁻¹)*	*NO_3^-–N (μg l⁻¹)*	*NH_4^+–N (μg l⁻¹)*	*SRP (μg l⁻¹)*	*DIN:SRP (g:g)*
Amos	4.3	8.12	120	4.11	33.9	520.6	214.4	20.3	3.6
Bothy	2	6.82	233	1.24	44.2	570.7	94.8	4.1	12.2
Changing	5.4	6.82	94	2.43	25.3	146.4	8.5	4.2	44.3
Emerald	15	6.62	67	1.33	23.4	97.3	10.3	2.1	33.6
Heywood	6.4	6.92	134	10.06	42.3	327	56.1	5.9	11.9
Knob	3.5	7.32	62	8.70	18.7	123.3	16.3	3.1	155.1
Light	4.4	6.82	121	9.21	44.1	33.4	11.2	4.7	31.9
Moss	10.4	6.82	40	1.85	23.2	111	5.6	1.4	50.7
Pumphouse	4	6.92	86	3.02	18.4	63.6	7.1	2.5	20.2
Sombre	11.2	6.82	78	3.99	25.8	181.9	12.9	4.6	74.9
Spirogyra	1.5	7.42	60	1.51	19.4	116.2	17.4	4.7	445.3
Tioga	4	7.42	134	4.29	20.9	105.7	53.3	6.1	5.7
Tranquil	8	6.92	52	1.53	16.7	80.7	1.8	2.7	275.0
Twisted	4	6.82	92	2.43	28.7	65.6	2.5	3.4	26.2

Adapted from Jones VJ, Juggins S, and Ellis-Evans C (1993) The relationship between water chemistry and surface sediment diatom assemblages in maritime Antarctic lakes. *Antarctic Science* 5(4): 339–348. Data averaged from collections during early winter, spring, summer open water between 1985 and 1991.

nutrient limitation (a ratio of ~7 represents balanced growth of phytoplankton). Marked seasonal variations in the abundance, composition, and productivity of phytoplankton, bacterioplankton and protozooplankton within Heywood lake have been shown to be correlated with the seasonality of both physical factors and nutrient levels. The biota within the lakes on Signy Island can be expected to continue changing in response to animal-induced nutrient loading.

In addition to the well documented increases in nutrient loading in many of the lakes on Signy Island, the air temperatures in this region have been rising by ~0.25 °C per decade, which has led to increasing lake water temperatures (0.6 °C per decade) and more ice-free days each year. The higher air temperatures have caused elevated ice melt in the lake catchments, leading to elevated phosphorus loading from soil leaching. Measurements of dissolved phosphorus and chlorophyll *a* increased fourfold between 1980 and 1995 in response to climate warming. These data clearly point to the sensitivity of polar lakes to climate change, where small changes in air temperature result in extreme ecological change.

Shirmacher Hills, Queen Maud Land, East Antarctica

Location Schirmacher Hills, located in the Central Queen Maud Land of East Antarctica, is an ice free area, bounded by a continental ice sheet on the south and the Fimbul ice-shelf on the north. The region is 17 km in length, 2–3 km wide and lies 100 km from the East Antarctic ice-sheet. Constituted by low lying hills that run East–West, the area varies widely in terms of elevation above sea level. The southern portion of the area is overlain by continental ice-sheet with recessional moraines and ice sheets descending onto bare rock. In contrast, the northern area exhibits steep escarpments all along its length in contact with the ice-shelf, an area often containing epishelf or tidal freshwater lakes similar to those that occur in the Bunger Hills. There are over 100 lakes and ponds of varying depths and melt-water streams in the area.

Formation and diversity The Schirmacher Hills contains several freshwater lakes formed by ice erosion and relict saline lakes formed as a result of the isolation of sea inlets and lagoons. The lakes are fed by melt water from snow beds and ice slopes during the summer.

Lakes Verkhneye, Pomornik, Glubokoye, and Stancionnoye lie in the eastern portion of the Shirmacher Hills and originate from glacial ice-scour. These lakes range in depth from 3 to 35 m. Lakes Untersee and Obersee are the two most studied lakes in the region and lie at elevations between 650 and 800 m. Lake Untersee (11.4 km^2) is a perennially ice-covered (~3 m ice cover), ultra-oligotrophic lake with a maximum depth of 169 m. About 2% of the incident sunlight reaches 145 m, making Lake Untersee one of the most transparent water bodies in the world. The water column throughout the majority of the lake is well mixed; however, there is a trough in the south-eastern portion of the lake that is physically and chemically stratified. The surface waters are supersaturated with oxygen, while water below 80 m is anoxic. High pH values (10–11) occur above 75 m, but decrease to ~7 at 100 m. Methanogenesis, methane oxidation, and sulphate reduction have all recently been measured in the deeper waters of this lake. Although smaller, Lake Obersee (3.4 km^2) shares many of the same physiochemical features (i.e., high pH, oxygen supersaturation, and high transparency of ice) with Lake Untersee.

Larsemann Hills

Location The Larsemann Hills (69°24′ S, 76°20′ E) are a series of rocky peninsulas and islands, located midway between the eastern extent of the Amery ice shelf and the southern boundary of the Vestfold Hills, in Prydz Bay, East Antarctica. Occupying an area of 50 km^2, the Larsemann Hills consist of two main peninsulas, Broknes to the east and Stornes to the west, as well as several off-shore islands. More than 150 freshwater lakes exist in the area, ranging from small ephemeral ponds to lakes exceeding 0.13 km^2 (Lake Nella) and 38 m deep (Progress Lake).

Formation and diversity The lakes in Larsemann Hills are thought to have formed from the exposure of basins after the retreat of the continental ice cap or after isolation due to the isostatic uplift following deglaciation. The lakes are connected to the coast by steep-sided valleys that dissect the area. During the summer months these lakes are partially to fully ice free and are well mixed by the strong easterly katabatic winds, while during the winter they lie under ice covers ~2 m thick. In general, the lakes on Stornes Peninsula have lower conductivities than those on Broknes Peninsula; these differences are believed to reflect the amount of freshwater input or the time elapsed since deglaciation. There is more snow cover on Stornes than Broknes Peninsula, which results in a cooler microclimate. Lake Reid (69°22′ S, 76°23′ E) on Broknes Peninsula is a relatively small (0.2 km^2), shallow lake (4 m deep), which is seasonally stratified and brackish. During winter the lake becomes anoxic, acquiring oxygen after ice melt and mixing in summer.

Vestfold Hills

Location The Vestfold Hills lie along the coast of Princess Elizabeth Land (68°25′–68°40′ S, 77°50′–77°35′ E) and occupy an area of ~410 km^2. The region and several outlying islands are typically snow free and contain ~150 freshwater and saline lakes, which account for 8% and 2% of the total area, respectively.

Formation and diversity Following the retreat of the continental ice sheet after the last glacial maximum ~12 000 years ago, isostatic rebound occurred at a faster rate than sea level rise. As the land rose, it cut off fjords and trapped pockets of seawater, creating lakes. The freshwater lakes include supraglacial and proglacial lakes, while the saline lakes range from brackish to hypersaline (6× seawater) and include both permanently stratified and seasonally mixed lakes. The lakes closest to the ice sheet are typically fresh, while those closer to the coast tend to be saline or hypersaline. The stratified lakes can be divided into different geographical regions: Long Peninsula, Broad Peninsula, Ellis Fjord, and Mule Peninsula.

Ace Lake, lying in the northern portion of the Vestfold Hills on Long Peninsula, 10 km from the ice sheet and 150 m from the sea, went through a complicated evolution, beginning as freshwater, which was then inundated by seawater, dried down and refilled by glacial melt water. The bottom saline waters and the upper fresh waters do not mix and the lake is permanently stratified. The lake is oligotrophic with a depth of 25 m, an area of 0.16 km^2 and a 1.5–2 m thick ice cover. The water below 12 m is permanently anoxic and contains sulfate reducing and methanogenic bacteria. Extensive studies have been carried out on Ace Lake and have shown that there are significant interannual variations in biological activity related to the ice cover and local meteorology.

Bunger Hills

Location The Bunger Hills is a rocky, ice-free area located in eastern Antarctica (66°17′ S) and is surrounded on all sides by glacial ice. This region is thus different from Vestfold Hills, which has the open ocean as one of its boundaries, but similar to Schirmacher Hills, which is also surrounded by glaciers. The total area is about 950 km^2, of which 420 km^2 is exposed rock. Most lake studies have occurred in the southern Bunger Hills, which has a maximum relief of about 160 m and is dissected by many steep valleys filled by lakes. Lakes also occur in the till-covered lowlands, but are generally smaller and more circular in shape. The climate of the Bunger Hills is similar to that of other rocky coastal areas of the East Antarctic coastline and most closely related to that of the Vestfold Hills.

Formation and diversity Over 200 water bodies occur in the Bunger Hills, ranging in size from small, shallow ponds that freeze to the bottom during winter, to Algae Lake, one of the largest and deepest surface freshwater lakes in Antarctica (14.3 km^2, 143 m deep). The conductivity of the lakes ranges from ultrafresh (<20 mg l^{-1} total dissolved solids (TDS)) for those which receive melt water from the Antarctic plateau, to highly mineralized (>80 g l^{-1}

TDS). Russian scientists working on these lakes characterized four types depending upon their hydrological and chemical characteristics (Table 3).

The lakes of the Bunger Hills differ from other coastal Antarctic lakes in the presence of a relatively high number of epishelf lakes. Owing to their position between land and a floating ice shelf or glacier, these lakes are tidal, containing a layer of freshwater overlying the water derived from the adjacent marine environment (Figure 2). The degree to which marine incursion occurs depends upon the actual hydraulic potential of the lake. Higher inflows produce hydrostatic pressure that minimizes the movement of marine water into the lake, whereas lower inflows allow marine water to enter the lake basin. Only about 10 known examples of this type of lake exist and are believed to have provided important refuges for aquatic organisms during glacial periods.

The biology of lakes in the Bunger Hills has received relatively little study to date. Research by Russian and Australian scientists revealed that the larger lakes have low water column primary production (0.08–326 mg carbon per cubic meter per day) and phytoplankton biomass (chlorophyll *a* is typically $<2\ \mu g\ l^{-1}$). The highest production occurs in lakes with the highest salinities. Despite low water column primary productivity, microbial mats exist in nearly all lakes of the Bunger Hills and consist of cyanobacteria, chlorophytes, diatoms, mosses, and heterotrophic grazers.

The McMurdo Region

Inland Lakes

Location The McMurdo Dry Valleys (MCM) (77°30′ S) of southern Victoria Land have a surface area of ~4000 km^2, representing the largest and most southerly ice-free area on the Antarctic continent (Figure 3). The MCM comprise three large valleys (Victoria, Wright, Taylor) along with many adjoining areas and consist of a mosaic of landscape features including glaciers, ephemeral streams, perennially ice-covered lakes, and exposed bedrock and soils. The region is ice-free because the Transantarctic Mountains block the flow of ice from the Polar Plateau and the warm katabatic winds flowing from the Polar Plateau to the sea through the east–west trending valleys lead to relatively high rates of ablation and associated ice loss. The largest lakes in this

Table 3 Characteristics of the major lakes within the Bunger Hills based on watershed type, and the geochemistry and physical properties within the lakes

Lake type	*Lake character*	*Examples*
Low water retention resulting from input from glacial melt	Low conductivity, typically isothermal	Algae Lake, Lake Dalekoje
Lakes of glacial origin with some through flow	Low to moderate conductivity, melt water dominated by land sources	Lake Dolgoe, Lake Dolinnoje
Lakes with a marine origin, often isolated from other hydraulic input	High conductivity, generally closed	Lake Polest, Lake Vostochnoye
Lakes with marine incursions (epishelf lakes)	Low salinity, tidal	Transkriptsii Gulf, Lake Pol'anskogo

Modified from Klokov V, Kaup E, Zierath R, and Haendel D (1990) Lakes of the Bunger Hills (East Antarctica): Chemical and ecological properties. *Polish Polar Research* 11: 147–159.

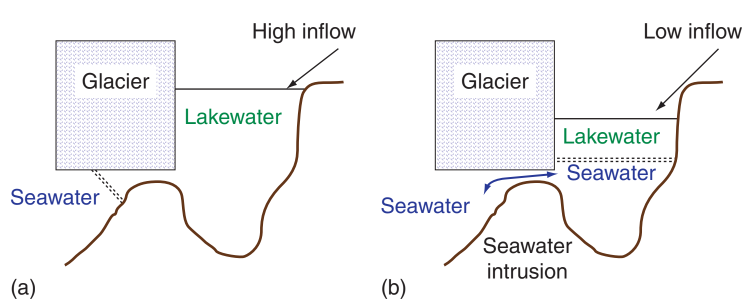

Figure 2 Conceptual diagram of the mixing dynamics in an epishelf lake. (a) High inflow rates keep seawater from entering the lake basin; (b) Low inflow allows seawater to enter the lake basin producing a two layer system with freshwater overlying a marine layer. The double dashed line depicts the interface between seawater and freshwater. Modified from Gibson JAE and Anderson DT (2002) Physical structure of epishelf lakes of the southern Bunger Hills, East Antarctica. *Antarctic Science* 14(3): 253–261.

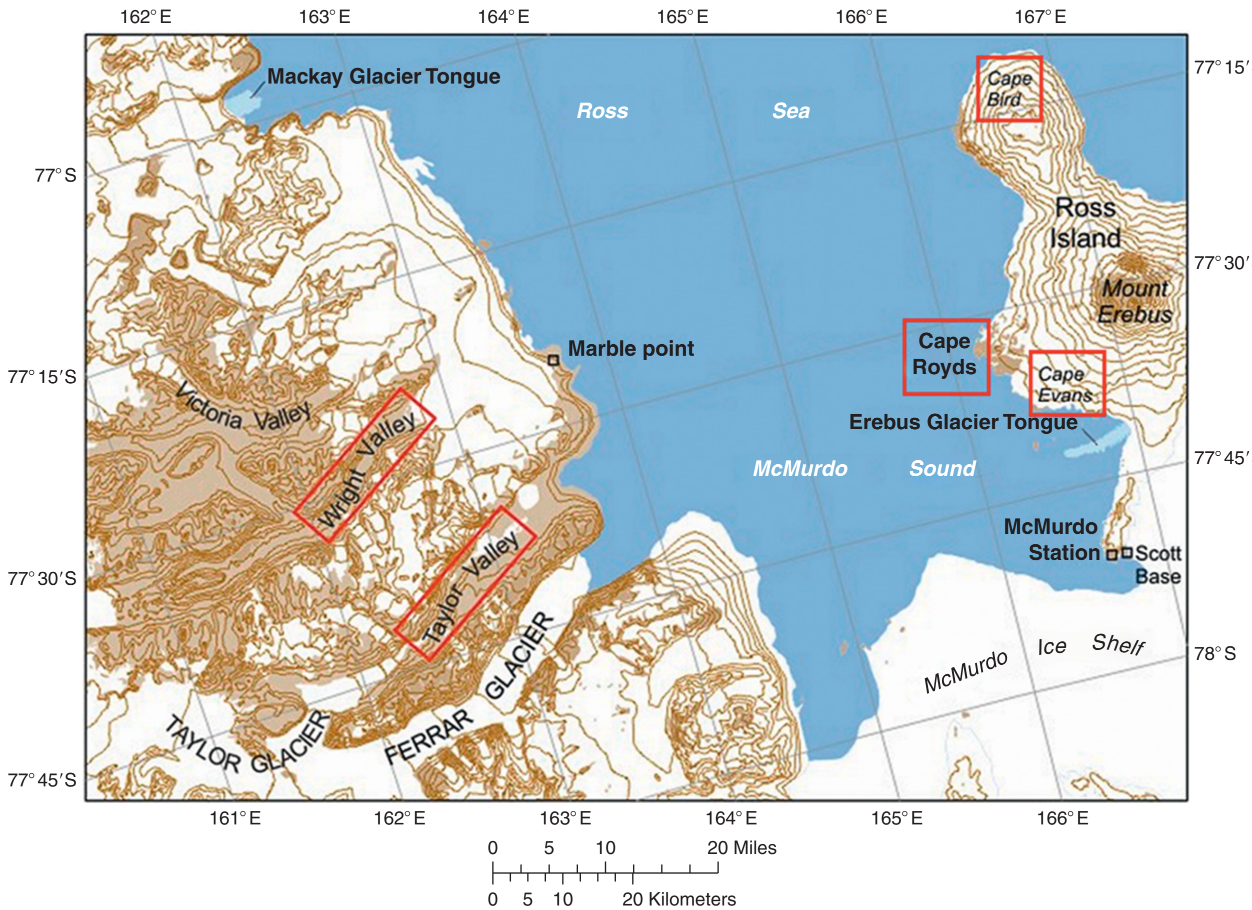

Figure 3 Locator map of the McMurdo Sound area showing the McMurdo Dry Valleys to the east (brown areas) along with the locations of the Wright and Taylor Valleys. The coastal lakes areas on Ross Island (Capes Byrd, Evans and Royds) are shown to the west. The red boxes denote regions containing lakes discussed in the manuscript.

area lie at the bottom of these valleys. The average annual temperature (~–18 °C) and precipitation (<5 cm water equivalents per year) make this ecosystem the coldest and driest of all lake regions in Antarctica. As a result, all lakes in the area are permanently ice-covered, except for a single pond (Don Juan Pond) where salinity is more than 18 times that of seawater.

Formation and diversity The McMurdo Dry Valleys contain eight relatively large lakes (Vida, Vanda, Fryxell, Hoare, Bonney, Joyce, Miers, and Trough) all of which have permanent ice covers ranging in thickness from ~4 to 7 m (Vida is an exception with a 18 m thick ice cover overlying saline – 5× seawater – water) and possess unique physical and geochemical attributes. Except for Lake Miers, all these lakes have closed basins with no surface outflow. Studies on these lakes began in 1957 as part of the IGY, and today, lakes in the Taylor Valley (78° S) form the centerpiece for the US National Science Foundation's MCM Long-Term Ecological Research (LTER), which has collected an extensive set of data on three of the lakes (Fryxell, Hoare, and Bonney) and the surrounding ecosystem, since 1993.

The lakes in the present day MCM evolved as the result of changing climate conditions since the last glacial maximum. Data from the Taylor Valley have shown that over the past ~20 000 years, lake levels within the MCM have varied considerably in relation to climate. Glacial Lake Washburn filled the entire Taylor Valley from the last glacial maximum to the early Holocene as a result of an ice dam formed at the base of the valley by the advancing West Antarctic Ice Sheet. As the climate became warm, the West Antarctic Ice Sheet retreated and Lake Washburn drained to McMurdo Sound, leaving behind smaller lakes in the lowest portions of the valley. Little is known about the limnology of these lakes but recent isotopic measurements show that many of the lakes in the MCM lost their ice covers and evaporated to small brine ponds or disappeared completely

~1200 years ago. A warmer climate since this period produced a flush of glacier melt that overflowed the brine ponds, producing the chemically stratified lakes we see today. The legacy of the ancient lake stands is now evident and relict resources left behind by these systems drive many of the biological processes within the MCM. For example, as the lakes rose, the soils inundated and became organic rich lake sediments, which became part of the terrestrial landscape as the lakes fell. The organic matter deposited during the period of inundation fuels much of the present day heterotrophic activity in the dry valley soils. These ancient, climate-driven lake-level changes also led to concentrated brine pools containing high levels of dissolved organic carbon, inorganic nitrogen, and inorganic phosphorus, which now form in the deep waters of many of the present lakes. The upward diffusion of these ancient nutrients has been shown to drive contemporary phytoplankton and bacterioplankton productivity. Owing to low rates of annual primary production resulting from the long polar night and low light penetration through the thick permanent ice covers during the austral summer, annual primary production to respiration ratios in Lake Bonney (and presumably other lakes in the area) are less than unity. Hence, these ancient nutrient pools are essential to contemporary life in the lakes – without them, biology would cease.

The deep-water salts in the lakes and ponds of Wright Valley (e.g., Lake Vanda, Don Juan Pond) are comprised of $CaCl_2$ whereas NaCl dominates the brines of lakes in the other valleys. The large differences in salinity and ionic composition of the lakes (Figure 4) are related, in part, to how the lakes have responded to temperature changes through the Holocene. Specifically, the difference in brine composition among lakes is related to the eutectic properties of NaCl and $CaCl_2$. The permanent ice-covers, low advective stream inflow (stream flow is low and exists for 4–6 weeks each year), and strong vertical chemical gradients that result from relatively young freshwater overlying ancient brines suppress vertical mixing in these lakes to the level of molecular diffusion. As a consequence, they have not mixed completely for thousands of years. The deep saline waters also trap and store solar energy in the chemically stratified lakes, producing deep warm waters that exceed 20 °C in Lake Vanda.

Biological measurements on these lakes reveal a truncated food web with relatively few metazoans

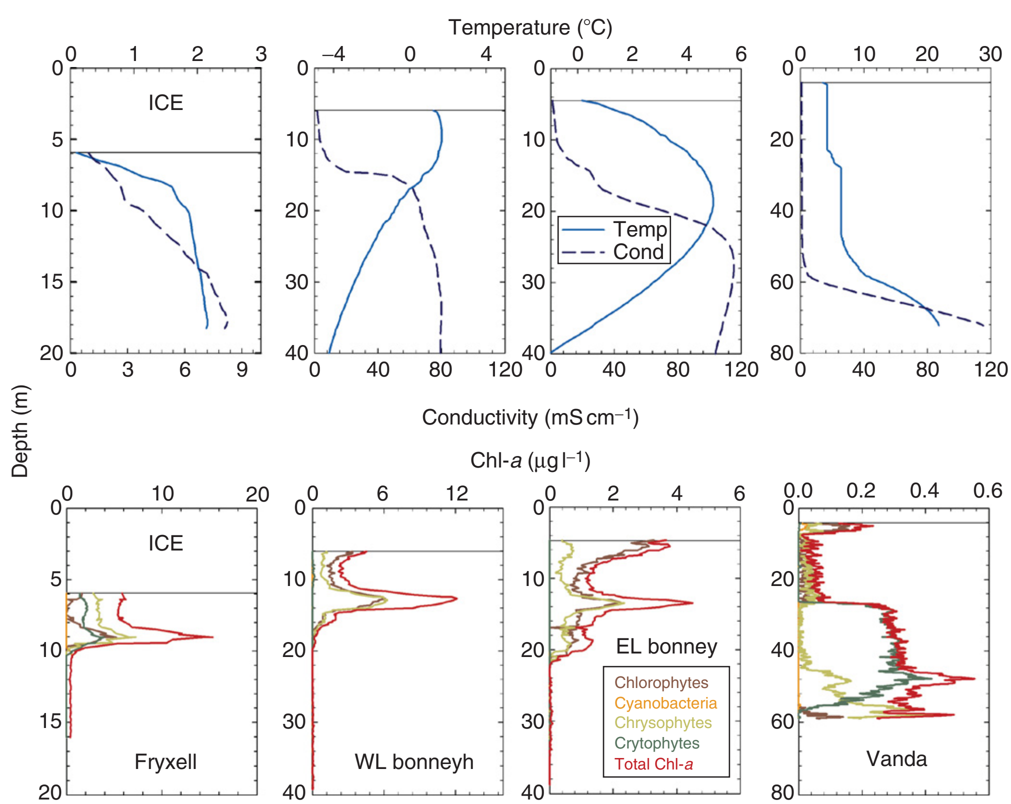

Figure 4 Temperature, conductivity, and chlorophyll *a* profiles for Lakes Fryxell, Bonney (west and east lobes), and Vanda in the McMurdo Dry Valleys. The chlorophyll *a* profiles, obtained with a spectral fluorometer, depict values for four algal groups as well as total chlorophyll *a*.

(primarily rotifers); the lakes completely lack crustaceous zooplankton and fish. The vertical zonation of phytoplankton reflects the lack of vertical mixing and the presence of strong chemical gradients. Figure 4 shows the strong vertical stratification of biomass and species composition through the water column, and the relationship between the deep-chlorophyll maxima and upward diffusion of ancient nutrient pools. A statistical comparison of the phytoplankton diversity among the lakes reveals that surface groups differ from the deep-living populations, and that the phytoplanktons in the lakes of the Taylor Valley differ from those in Lake Vanda in the Wright Valley. This pattern reflects the chemical evolution of these lake ecosystems.

Unlike the temperature regime on Signy Island, air temperatures in the MCM have come down at an average rate of 0.8 °C per decade over the past two decades. This cooling trend has led to the formation of thicker ice covers on the MCM lakes and decreased light penetration to the water column (0.055mol photons per square meter per day annually in west lobe Lake Bonney). Because phytoplankton photosynthesis in the lakes is light limited, phototrophic primary production has decreased by 50% over the past 10 years in response to higher light attenuation by the thicker ice covers (Figure 5). The increasing trend in chlorophyll *a* after 2001 is the result of nutrient enrichment following an unusually warm year. Continued cooling in this region will clearly produce a cascade of ecological changes within the MCM lake ecosystems as phototrophic primary production decreases even further.

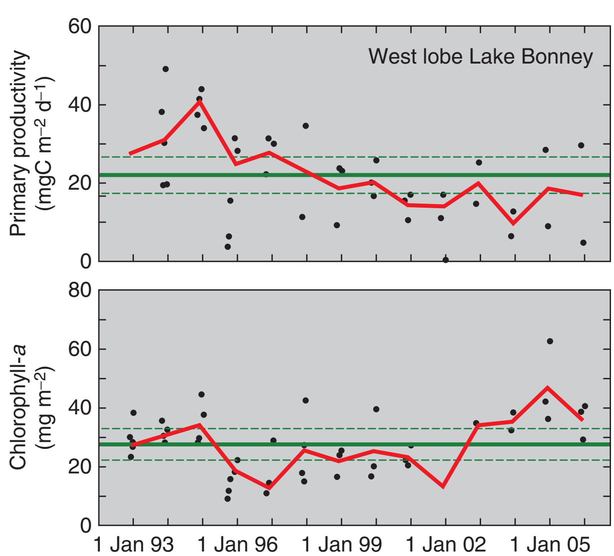

Figure 5 Long-term trends in depth integrated primary productivity and chlorophyll-*a* in the west lobe of Lake Bonney. Black circles represent data from all dates where measurements were made; the solid red line shows the long-term trend in average values for November and December. The solid and dashed green lines denote the mean and 95% confidence intervals around the November and December trend.

Coastal Ponds

Location Coastal lakes and ponds are distributed around the margins of the Antarctic continent, and are particularly abundant around the ice free areas of McMurdo Sound. These shallow coastal aquatic systems typically freeze solid over the winter months and cryoconcentrate the organisms in the ice, forcing the majority of the organisms, gases, and dissolved organic matter to the bottom (Figure 6). Most of the lakes studied are on Ross Island, east of McMurdo Sound near capes Evans, Royds and Bird.

Formation and diversity The coastal lakes and ponds occupy ice gouged areas in close proximity to McMurdo Sound (Figure 3). The main glacial groove in which the majority of the larger lakes at Cape Royds lie runs from Backdoor Bay along Blue Lake and branches off towards the coast with Clear, Coast, and Pony lakes. Two lakes at Cape Barnes, Sunk Lake, and Deep Lake, are found in a continuation of this same groove. These lakes range from freshwater to brackish with the ionic content enriched by precipitation, wind blown salt spray from the nearby sea, leaching from the volcanic rocks, and biologic inputs from penguins and sea birds. During the summer months, these ponds undergo varying degrees of melt depending upon snowpack and climatic conditions. The organisms that live in these coastal ponds experience extreme and often abrupt changes in light, temperature, water availability, salinity, and nutrients in contrast to those that live in the more stable inland meromictic lakes (Table 4).

Pony Lake is a shallow, eutrophic coastal pond located on Cape Royds. This lake is ice-covered except in mid-summer, when strong winds cause complete mixing of the water column. The lake is ~120 m long and 70 m wide, and 1–2 m deep. The source of water is snow, and water is lost by both ablation (from the snow and ice cover) and evaporation in mid-summer. Ice cover typically persists until late December. The pond is saline (~0.21 ppt), as a result of proximity to the sea and accumulation of salts by ablation. Phytoplankton are abundant (Chl *a* 28–140 $\mu g\ l^{-1}$) with the dominant alga being the chlorophyte *Chlamydomonas intermedia*. There is a penguin rookery along the eastern shore and the lake has high nutrient concentrations. DOC concentrations range from 10 mg carbon per liter during the early season to as high as 110 mg carbon per liter during the height of the algal blooms.

Figure 6 Ice core being collected from Pony Lake, with inset on left showing the bottom portion of the core where organisms, gases and organic matter cryo-concentrate.

Table 4 Comparison of ecological parameters in phytoplankton communities of Antarctic coastal ponds (i.e., Pony Lake, Blue Lake) and inland meromictic lakes (i.e., Lake Bonney, Lake Vanda)

Parameter	*Coastal lakes and ponds*	*Meromictic lakes*
Habitat stability	Low, experiences catastrophic changes	High, predictable
Growth season	Weeks	Months
Nutrient supply	High, C, N, P in excess	Low, growth limiting
Strategies	*r*-Selection (opportunistic, fast growing, rapid population shifts)	*K*-selection (in equilibrium highly efficient, slow population shifts)
Niche breadth	Wide, broad tolerances	Narrow, specialists
Species diversity	Low	High
Productivity	High	Low

Adapted from Vincent WF and Vincent CL (1982) Response to nutrient enrichment by the plankton of Antarctic coastal lakes and the inshore Ross Sea. *Polar Biology* 1: 159–165.

Conclusions

Despite temperatures well below the freezing point, the Antarctic continent possesses a wide variety of lakes (Figure 7) that contain liquid water throughout the year, making them an oasis for life in what would otherwise appear to be an uninhabitable environment. Interestingly, owing to their sensitivity to climate changes (small climate changes produce a magnified cascade of physical, chemical and biological changes), these lakes receive relatively little discussion in limnology textbooks. Antarctic lakes contain reservoirs of the evolutionary history of the continent and the contemporary activity we measure today often reflects the legacy of resources deposited in the environment during the evolution of the lake basins. Subglacial lakes, which have been isolated beneath the Antarctic ice sheet for >10 My, present an exciting new paradigm for limnologists. Recent calculations show that the subglacial lakes and rivers beneath the Antarctic ice sheet contain ~10 000 km^3 of liquid water. This volume is ~10% of all lake water on Earth, enough to cover the whole continent with a uniform water layer with a thickness of ~1 m. Once sampled, information from these systems will change the way we view global water and biological reservoirs on our planet. Importantly, lakes in Antarctica provide clues on ecosystem properties and metabolic lifestyles that may exist on other frozen worlds such as Mars and Europa. As such, they provide us with a logical step in our search for extraterrestrial life.

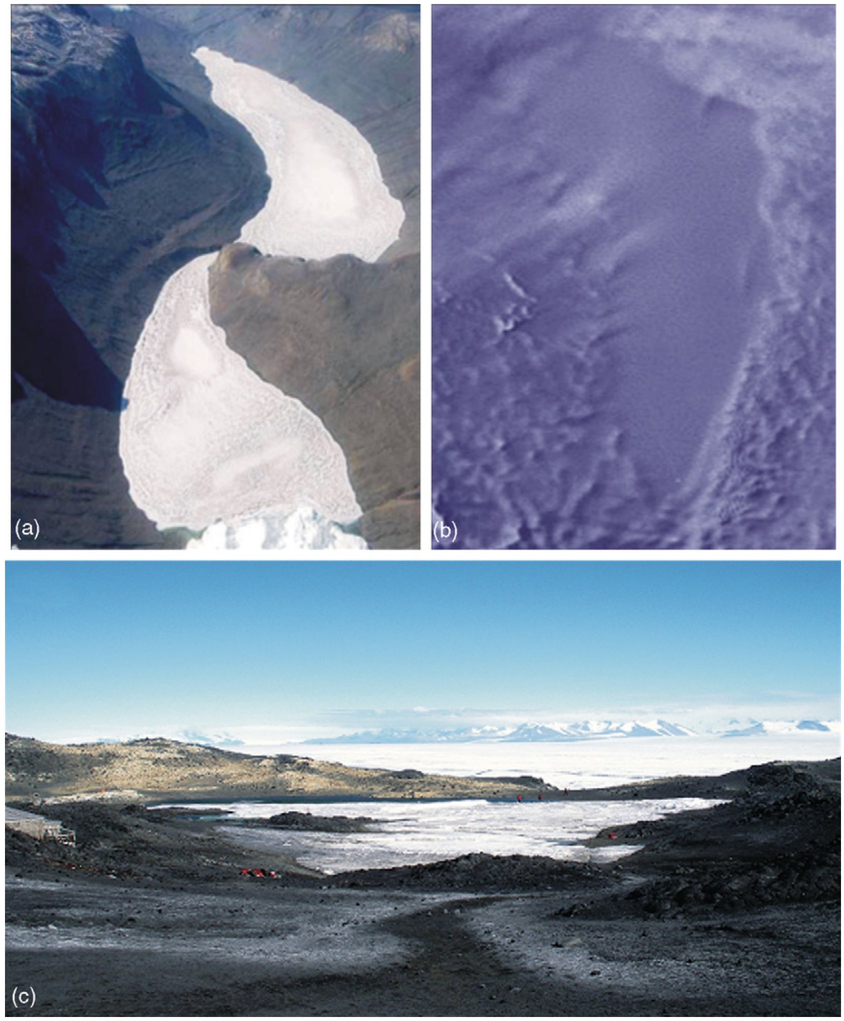

Figure 7 Examples of different Antarctic lake types: (a) Lake Bonney an epiglacial lake, located in the McMurdo Dry Valleys is bound by both rock and glacier; the Taylor Glacier forms the lower boundary of the lake in the photo; (b) Radarsat image showing the flat area on the surface of the East Antarctic Ice sheet where the ice sheet 'floats' as it passes over the waters of Subglacial Lake Vostok; (c) Pony Lake is a shallow coastal lake at Cape Royds that freezes to the bottom in winter. Radarsat image is courtesy of NASA-GSFC. Shadows on the mountain side appear as dark blue areas in panel (a) and should not be confused with liquid water or dark mineral deposits.

See also: Biodiversity of Aquatic Ecosystems; Effects of Climate Change on Lakes; Meromictic Lakes; Origins of Types of Lake Basins; Phytoplankton Nutrition and Related Mixotrophy; Saline Inland Waters.

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